Symposium: Interactions of Mycorrhizal Fungi

The Role of Phosphorus Nutrition in Interactions of Vesicular-Arbuscular Mycorrhizal Fungi with Soilborne Nematodes and Fungi

G. S. Smith

Research plant pathologist, Agricultural Research Service, U. S. Horticultural Research Laboratory, 2120 Camden Road, Orlando, FL 32803. Present address of the author: Texas A & I Citrus Center, Weslaco, TX 78596.
I thank J. H. Graham for his assistance with this manuscript.
Accepted for publication 27 August 1987 (submitted for electronic processing).

Vesicular-arbuscular mycorrhizal (VAM) fungi form a symbiotic relationship with their host by colonizing the cortical region of feeder roots both inter- and intracellularly. They benefit the host plant primarily by increasing the capability of the root system to absorb and translocate phosphorus (P) and minor elements through an extensive network of hyphae external to the root (10,15,16,23). The near ubiquitous occurrence of VAM fungi in roots of agricultural crops and their obligate dependence on the host have resulted in a common association with plant-parasitic nematodes and root-infecting fungi. In fact, concomitant infections of VAM fungi and pathogens in host roots are the rule rather than the exception.

Research on the potential of VAM fungi to limit yield reductions and pathogen activities has been largely restricted to greenhouse studies conducted in sterilized, P-deficient soils to maximize plant growth stimulation by the VAM fungus. Because interactions varied with the specific host-symbiont-pathogen combination, generalizations on the effect of VAM fungi on disease were difficult (17,26,27). Disease severity or pathogen activities could be increased, decreased, or not affected by the presence of the VAM fungus. In their review of mycorrhiza-nematode interactions, however, Hussey and Roncadori (17) noted that the single most common effect of VAM fungi on nematode-susceptible plants was to increase tolerance. The need for field research and a greater emphasis on the role of P in the host-symbiont pathogen relationship was stressed.

Because so few studies had investigated the role of P nutrition, it was not possible to conclude whether responses of mycorrhizal plants to pathogens differed from nonmycorrhizal plants at a comparable nutritional status. In addition, most studies were single-factor descriptive experiments of an exploratory nature (32). Interactions between the VAM fungus and pathogen could not be verified because either interaction components were not present in the experimental design or they were not derived.

Recently, interaction experiments in moderate to highly fertile soils have avoided large growth disparities between mycorrhizal and nonmycorrhizal plants (3,4,8,13,14,28,30,33). Field experiments have also been conducted on a limited basis (25,29). The intent of this review is to examine those studies that compared the influence of P nutrition with VAM fungi on the host-pathogen relationship. Additionally, methods for conducting studies of host VAM fungi-pathogen interactions will be discussed and hypotheses presented on mechanisms that mediate these interactions.

TROPHIC RELATIONSHIPS

The potential for interaction in the host-mycorrhiza-pathogen relationship can be considered in relation to the trophic classifications of VAM fungi, plant-parasitic nematodes, and root-infecting fungi (5,9,31). VAM fungi are obligate biotrophs requiring living host cells to obtain organic nutrients (15,24). The host-mycorrhizal relationship in vivo is most often mutualistic. Plant-parasitic nematodes are antagonistic, obligate biotrophs and are classified according to their feeding habits in roots. Sedentary endoparasites become immobile as adults and depend on specialized transfer cells for nourishment, whereas migratory endo- and ectoparasites obtain nutrients by piercing cortical parenchyma cells with their stylet and ingesting the cytoplasm (17,31). Pathogenic root-infecting fungi may be antagonistic, facultative saprotrophs with some root-rotting fungi capable of feeding as necrotrophs. They are commonly classified as wilt pathogens, e.g., *Fusarium*, *Verticillium*, or root-rotting pathogens, e.g., *Phytophthora*, *Gaeumannomyces*, *Fusarium*, and *Rhizoctonia* (9). The potential for VAM fungi to affect a host-pathogen relationship by mechanisms unrelated to improved P nutrition is hypothesized to be greatest with obligate biotrophs and least with facultative saprotrophs. Specific mechanisms for these interactions will be discussed in a later section.

This article is in the public domain and not copyrightable. It may be freely reprinted with customary crediting of the source. The American Phytopathological Society, 1988.

PATHOGEN INTERACTIONS WITH VAM FUNGI AND P NUTRITION

The use of P-fertilized, nonmycorrhizal controls of similar size and nutritional status as mycorrhizal plants is fundamental to determining whether mycorrhiza-pathogen interactions are unrelated to improved P nutrition. Nonmycorrhizal plants similar in form and major element nutrition to mycorrhizal plants can be obtained, although they may differ in function and micronutrient content (21).

Interactions with plant-parasitic nematodes. Our understanding of the role of P nutrition in mycorrhiza-nematode interactions has been expanded by recent greenhouse and field studies with sedentary endoparasitic nematodes. The predominant effect of VAM fungi on nematode-susceptible plants in greenhouse studies continues to be increased tolerance, and this effect can be duplicated with soil P amendments. In field microplots, however, the severity of root-knot nematode damage on cotton was greater on P-fertilized, nonmycorrhizal plants than mycorrhizal plants at P levels deemed adequate to high for cotton production (30). This effect was attributed to zinc deficiency induced by nematode infection and high soil P levels. High levels of P fertilization inhibit zinc uptake (20); apparently VAM fungi can alleviate this P-induced zinc deficiency and, thus, increase host tolerance to nematode parasitism.

Investigations of penetration and infection frequencies, reproduction, and developmental life stages of the nematode as opposed to host response have provided a clearer insight into the non-P-nutritional and P-nutritional effects of mycorrhizal root colonization. Also, mycorrhizal effects on nematode activities are usually more pronounced when plants are preinoculated with VAM fungi (6,30).

Mycorrhizal fungi do not appear to affect penetration and infection processes differently from P. The number of nematodes penetrating and infecting a root system or egg production has been greater when root weights were increased by VAM fungi or P fertilization (3,14,29,30,33). Also, higher infection densities on roots were reported on mycorrhizal and P-fertilized cotton roots from field microplots (29). When penetration or infection frequencies were lower on mycorrhizal root systems compared with nonmycorrhizal root systems, however, the effect was temporally related (3,28). Penetration was lower only at 3 days after nematode inoculation on mycorrhizal onion roots, whereas lowered infection of mycorrhizal cotton roots did not occur until 14–28 days after nematode inoculation. Total egg production has not been related to the number of eggs per ovipositing female, except in one study on first generation females infecting P-fertilized nonmycorrhizal cotton (28).

Apparent reductions in nematode infection or reproduction by VAM fungi are often demonstrated by expressing root population densities of nematodes or eggs on a per gram root weight basis. Results should be carefully interpreted when these parameters are presented as the sole measure of mycorrhizal suppression of nematode activities. The consideration of nutritional and plant growth effects by VAM fungi is essential because fewer nematodes or eggs per gram root on larger mycorrhizal root systems may be a result of dilution of the root population density of the nematode. This phenomenon could better be characterized as a form of disease escape due to increased root growth rather than to direct suppression of nematode activities by VAM fungi.

The differentiation of mycorrhizal effects from P-nutritional effects has been most clearly demonstrated from measurements of nematode development, expressed as number of adults or frequency counts of life stages, on mycorrhizal and P-fertilized, nonmycorrhizal root systems (6,14,19,28). Only on tomato was nematode development reported to be unaffected by VAM fungi or P (30). Generally, P fertilization stimulates nematode development when compared with a P-deficient plant. On mycorrhizal root systems, however, development is inhibited (6,14,19,28) unless mycorrhizal plants are grown in extremely P-deficient soil (6).

Interactions with soilborne fungal pathogens. Host response and fungal infection of mycorrhizal plants have been found to be similar to those of P-fertilized, nonmycorrhizal plants (7,8,13), except in one case, where disease severity was unaffected by P fertilization but reduced by a VAM fungus (4). The effects of mycorrhizal root colonization on the cotton-Verticillium wilt and citrus-Phytophthora root rot relationships were considered a direct result of improved P nutrition (7,8). On cotton, plant growth suppression, vascular discoloration index, and Verticillium propagules per gram of petiole tissue were similar on mycorrhizal plants grown at 20 mg of P per kilogram of soil and similar-sized, nonmycorrhizal plants grown at 300 mg of P per kilogram of soil (8). On citrus, host tolerance to Phytophthora root rot was unaffected by VAM fungi in soil containing 6 mg of P per kilogram of soil, while mycorrhizal plants grown in soil containing 56 or 600 mg of P per kilogram of soil were less tolerant of root rot than nonmycorrhizal plants (7). The reduced tolerance on mycorrhizal plants was attributed to competition for similar host tissues. This explanation is consistent with the fact that both organisms infect cortical cells in feeder roots. Davis and Menge (7), however, concluded that the increased tolerance of P-fertilized, nonmycorrhizal plants may be due to the inhibition of zoospore release from sporangia. Based on results from an in vitro bioassay, zoospore release from sporangia was inhibited by concentrations of phosphate ions in solution greater than 1.6 mg/L. Because soil solution P concentrations seldom exceed 1.6 mg/L even in fertile soils (2), this hypothesis would have been more tenable if inhibition of zoospore release could have been demonstrated in soil solution extracts from P-fertilized soil sampled during the course of the experiment.

An increase in the level of host resistance in mycorrhizal wheat to take-all disease was also attributed to improved P nutrition (13). This effect is consistent with the recognition that take-all disease is favored by inadequate plant nutrition, especially P deficiency (9). High levels of VAM root colonization in plants grown in a P-deficient soil (0.5 mg of P per kilogram of soil) or the addition of 50 mg of P per kilogram of soil equally suppressed disease severity. This suppression was attributed to the improved root P status and a corresponding decrease in root exudation.

By contrast, the effect of P concentration in a soilless substrate on Fusarium crown and root rot of tomato differed from that of a VAM fungus (4). For nonmycorrhizal plants, increasing levels of available P in the substrate, as well as an increase in the P content of shoots and roots, had no effect on shoot growth, percentage of root necrosis, or final propagule density of *Fusarium oxysporum* f. sp. *radicis-lycopersici*. Root necrosis and *Fusarium* propagule density on mycorrhizal root systems, however, were reduced at all P levels even though percentage VAM root colonization varied from 8 to 65%. No explanation was offered for the observed limitation in disease and pathogen development on mycorrhizal plants. This report that equivalent reductions in pathogen activities are independent of the level of mycorrhizal root colonization, however, contrasts with the hypothesis that threshold levels of VAM fungal root colonization are required to affect plant growth responses and pathogen activities (8,13,28,33).

METHODS FOR STUDYING MYCORRHIZA-PATHOGEN INTERACTIONS

In spite of the large number of mycorrhiza-pathogen studies, our understanding of the relationship of P nutrition to the mycorrhizal component in the host-symbiont-pathogen relationship is incomplete. Research is needed to assess how VAM fungi affect the host-pathogen relationship differently from P. Methods used in pathogen-pathogen interactions (1,9,31) that have been adapted to mycorrhiza-pathogen interactions will be briefly discussed.

Host-symbiont-soil fertility. Growth responses to VAM fungi vary depending on the mycorrhizal dependency of the host, the endophyte species or strain, and the soil fertility level (10,15,16). Preliminary or exploratory research to determine whether an interaction is present should be conducted with a VAM fungal species or mixture of species that are indigenous to an area, extensively colonize roots, and stimulate plant growth at moderately fertile soil levels for the crop under study. This allows

for a closer approximation of the mycorrhizal plant's response to pathogen infection for the soil type and fertility level occurring in the field.

Research on mycorrhiza-pathogen interactions should avoid the exclusive use of soils deficient in P or with P levels below that used in normal production practices for the particular crop. A better approach would be to use varying soil P levels that encompass field recommendations to produce nonmycorrhizal plants of equivalent size and similar P nutritional status as mycorrhizal plants. These conditions are necessary to determine whether increased host tolerance of mycorrhizal plants is more than improved host vigor that can be mimicked by improved P nutrition alone. Because the majority of mycorrhiza-pathogen interactions have been conducted in P-deficient soils, the mycorrhizal effects on host response and pathogen acvtivities could have been confounded with P nutrition. Nutritional deficiences can profoundly affect host-pathogen relationships (1,9,11). Nonmycorrhizal plants grown in P-deficient, pathogen-infested soils generally have severely stunted root systems that affect the level of pathogen development and disease expression; comparisons with nutritionally superior mycorrhizal plants are inappropriate, and extrapolation to field situations untenable (17,27).

Initial inoculum density and inoculation sequence of pathogen and symbiont. Experiments to study the host response and pathogen activities on mycorrhizal and nonmycorrhizal, P-fertilized plants should use varied initial inoculum densities (Pi) of the pathogen in order to detect interactions (32). Use of varying Pi to produce different levels of disease incidence or yield reduction, however, should avoid the use of a Pi that so severely stunts or kills plants that mycorrhizal fungi are not given an opportunity to colonize roots and stimulate growth (19).

Because root infection by fungal and nematode pathogens precedes mycorrhizal root colonization (18), the sequence in which plants are inoculated with a pathogen relative to the time of VAM fungal inoculation may affect the nature of the interaction (17,27). Thus, an inoculation method used in many studies has been to precolonize plants with the VAM fungus 2–4 wk before pathogen inoculation (6,7,14,19,28,30). This technique allows VAM fungi time to colonize roots before they are challenged with the pathogen. Although precolonization with VAM fungi may represent an artificial system that favors the mycorrhizal relationship in those plants that are direct seeded into field soils, it is a realistic system for containerized or transplanted hosts that can be inoculated with VAM fungi before they are planted into field soil (17). This method has also been used in mycorrhiza-nematode interactions to simulate the effects of mycorrhiza on infection and development of secondary nematode generations (28).

Although the use of varying inoculum levels of the VAM fungus generally has not been considered an important factor because of the slow colonization rate of the symbiont, it seems logical that a minimum level of VAM fungal root colonization is required to affect pathogen activities. Thus, VAM fungal Pi of 0.5–5.0 spores per gram of soil has been used to produce optimal growth responses and maximum root colonization levels. Although thresholds of VAM fungal root colonization to affect nematode activities have been reported (14,28,33), high levels of VAM fungal root colonization have not reduced the degree of root infection by fungal pathogens (7,8,13,25).

Statistical models for mycorrhiza-pathogen interaction. Future research should depart from the more commonly used single-factor descriptive associations and employ statistical models containing interaction components to enhance interpretation of results (32). Factoral or regression analyses that evaluate the response of qualitative treatments (mycorrhizal versus nonmycorrhizal plants receiving a specified P regime) over varying quantitative treatments (pathogen Pi) are suitable for detecting statistical interactions. Also, frequency counts of nematode life stages over physiological time have been used to compare the effects of VAM fungi and P nutrition on nematode parasitism (19,28). Another quantitative approach adaptable to mycorrhiza-nematode interactions is the Seinhorst damage function, $Y = m + (1 - m)Z^{P-T}$, to determine if the model parameters T (tolerance limit), m (minimum yield), or Z (nematode virulence) are affected differently in mycorrhizal and nonmycorrhizal, P-fertilized plants (31,32).

MECHANISMS MEDIATING MYCORRHIZA-PATHOGEN INTERACTIONS

Hypotheses proposed to explain VAM fungal effects on soilborne plant pathogens generally have been considered to have either a physical or physiological basis (17,18). VAM fungi have been shown to affect root growth, root exudation, nutrient absorption, and host physiological responses to environmental stresses. Many of these factors are related to P physiology and nutrition (10,12,16,21,23). VAM fungi have not been shown, however, to interact directly with pathogens through antagonism, antibiosis, or predation. (1). More likely they indirectly affect the host-pathogen relationship by physiologically altering the host or by competing for space or host resources. Although these hypotheses are not all-inclusive and most are not supported by research data, they offer a basis for discussion and direction of future research.

Increased root growth and function. VAM fungi, through an increase in P nutrition, enhance root growth, expand the absorptive capacity of the root system for nutrients and water, and affect cellular processes in roots (15,16,24). These mycorrhizal-induced compensatory processes may explain the increased tolerance of mycorrhizal and P-fertilized plants because many plants can compensate for loss of root mass or function caused by pathogens (31). In fact, greater tolerance has been attributed to increased root growth and nutrient P status (3,17,30).

Nutritional effects other than P. VAM fungi can enhance the uptake of Ca, Cu, Mn, S, and Zn in addition to P (10,16,21). Host susceptibility to infection by pathogens and tolerance of the disease process can be influenced by the nutritional status of the host and fertility status of the soil (1,9,31). For example, nematode-damaged plants frequently show deficiences of B, N, Fe, Mg, and Zn (11). Also, high levels of P fertilization in the absence of VAM fungi can interact with minor element nutrition creating deficiences and predisposing plants to root-knot nematodes (29). Thus, VAM fungi may increase host tolerance to pathogens by increasing uptake of essential nutrients other than P that would be deficient in a nonmycorrhizal plant.

Alteration in root exudation. Because of the well-documented relationship between root exudation and root disease initiation (1,9), the influence of VAM fungi and P nutrition on root exudation as a regulatory process in root disease has been investigated (12,13). Changes in exudation patterns can affect fungal spore germination and root penetration, alter chemotatic attraction of nematodes to roots, and affect eclosion in those nematode species that require a hatching stimulus (1,9,31). The influence of P nutrition on membrane permeability in root cells and concentration and exudation of amino acids and reducing sugars has been proposed as a mechanism regulating mycorrhizal root penetration and colonization (23). VAM infection in P-deficient plants affected membrane permeability and exudation patterns similar to P fertilization in nonmycorrhizal plants. Improved nutritional status of the host by VAM fungal root colonization may affect qualitative or quantitative changes in root exudates to alter rhizosphere or rhizoplane microbial populations and population densities (18,24). If VAM fungi affect pathogen activities differently than P, then some aspect of root exudation (carbon utilization or allocation, microbial population shifts) unique to mycorrhizal root systems must be demonstrated.

VAM fungi have reduced nematode infection and development on several hosts in spite of larger root systems on mycorrhizal plants (6,14,28). The novel or increased production or shift in quantity of a particular compound that renders roots less attractive to pathogens or that alters microbial rhizosphere or rhizoplane populations that are inhibitory to pathogens are intriguing possibilities that warrant additional research.

Competition for host photosynthates. VAM fungi are almost totally dependent on soluble carbohydrates produced by the host

for their carbon source (15,24). Estimates of the energy cost of symbiosis to the host range from 4 to 17% (15,22). These carbon demands can inhibit plant growth under stress conditions of low light intensity, high levels of root colonization in a seedling plant, and low soil temperatures (16). Although evidence of host resource competition between VAM fungi and pathogens is lacking, this hypothesis warrants investigation, especially in interactions with sedentary endoparasitic nematodes, because of the obligate requirements of both groups of organisms for host derived compounds.

Radioactive isotope labelling has been used to quantify carbon flow in the mycorrhizal-*Bradyrhizobium*-bean relationship (22). Similar methods have been applied to study P absorption and translocation by VAM fungi (10,16). These techniques can be adapted to study carbon and phosphorus flow in a mycorrhiza-sedentary endoparasitic nematode relationship. Mechanisms affecting nematode activities in a mycorrhizal root system that are not related to improved P nutrition or increased photosynthesis may involve utilization of photosynthates by the VAM fungus at the expense of nematode development or reproduction, or conversion of carbohydrates received from the host into forms not usable by the nematode. Similarly, P transport by VAM fungi to the Casparian strip in roots is via fungal structures (24). This contrasts with mass flow and diffusion of P through soil and root symplast on a nonmycorrhizal root (2). Sequestering of P in fungal structures before transport to the host may restrict the availability of P for nematode development or reproduction.

Competition for space or infection site. Because VAM fungi, soilborne fungal pathogens, and plant-parasitic nematodes occupy similar root tissues, direct competition for space has been postulated as a mechanism of pathogen inhibition by VAM fungi (7,17,18). Competition between a VAM fungus and *P. parasitica* was proposed on citrus (7). On split-root systems, the amount of mycorrhizal colonized root tissue was reduced only when the VAM fungus and *P. parasitica* were in direct association. However, this hypothesis has not received much attention because root infection by pathogens precedes mycorrhizal root colonization, and many root pathogens infect at the root tip where VAM fungal structures do not occur (9,15,18). Actually, VAM fungi may provide more root tissue for pathogen infection by increasing root growth due to improved P nutrition (387,17). This hypothesis has been further discounted because inhibition of nematode activities on mycorrhizal root systems has occurred with approximately 50% of the root system devoid of any mycorrhizal structures (6,28,33).

CONCLUSIONS

With few exceptions the primary effects of mycorrhizal symbiosis on the host-pathogen relationship have been intimately related to improved P nutrition because substitution of VAM fungi with P fertilizers paralleled the mycorrhizal host response. However, several recent interaction studies with sedentary endoparasitic nematodes have provided the most convincing evidence that VAM fungi may affect the host-pathogen relationship differently than P. The clarification on nonnutritional effects of VAM fungi on this group of plant-parasistic nematodes may yield more definitive results because of the obligately biotrophic requirements shared by these two groups of organisms.

LITERATURE CITED

1. Baker, K. F., and Cook, R. J. 1982. Biological Control of Plant Pathogens. The American Phytopathological Society, St. Paul, MN. 433 pp.
2. Bieliski, R. L. 1973. Phosphate pools, phosphate transport, and phosphate availability. Annu. Rev. Plant Physiol. 24:225-252.
3. Cameron, G. C. 1986. Interactions between two vesicular-arbuscular mycorrhizal fungi, the soybean cyst nematode, and phosphorus fertility on two soybean cultivars. M. S. thesis. University of Georgia, Athens. 38 pp.
4. Caron, M., Fortin, A., and Richard, C. 1986. Effect of phosphorus concentration and *Glomus intraradices* on Fusarium crown and root rot of tomatoes. Phytopathology 76:942-946.
5. Cooke, R. 1977. The Biology of Symbiotic Fungi. John Wiley & Sons, London. 282 pp.
6. Cooper, K. M., and Grandison, G. S. 1986. Interaction of vesicular-arbuscular mycorrhizal fungi and root-knot nematode on cultivars of tomato and white clover susceptible to *Meloidogyne hapla*. Ann. Appl. Biol. 108:555-565.
7. Davis, R. M., and Menge, J. A. 1980. Influence of *Glomus fasciculatus* and soil phosphorus on Phytophthora root rot of citrus. Phytopathology 70:447-452.
8. Davis, R. M., Menge, J. A., and Erwin, D. C. 1979. Influence of *Glomus fasciculatus* and soil phosphorus on Verticillium wilt of cotton. Phytopathology 69:453-456.
9. Garrett, S. D. 1970. Pathogenic Root-Infecting Fungi. The University Press, Cambridge. 294 pp.
10. Gerdemann, J. W. 1968. Vesicular-arbuscular mycorrhiza and plant growth. Annu. Rev. Phytopathol. 6:397-418.
11. Good, J. M. 1968. Relation of plant-parasitic nematodes to soil management practices. Pages 113-138 in: Tropical Nematology. G. C. Smart and V. G. Perry, eds. University of Florida, Gainesville. 152 pp.
12. Graham, J. H., Leonard, R. T., and Menge, J. A. 1981. Membrane-mediated decreases in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. Plant Physiol. 68:548-552.
13. Graham, J. H., and Menge, J. A. 1982. Influence of vesicular-arbuscular mycorrhizae and soil phosphorus on take-all disease of wheat. Phytopathology 72:95-98.
14. Grandison, G. S., and Cooper, K. M. 1986. Interactions of vesicular-arbuscular mycorrhizae and cultivars of alfalfa susceptible and resistant to *Meloidogyne hapla*. J. Nematol. 18:141-149.
15. Harley, J. L., and Smith, S. E. 1983. Mycorrhizal Symbiosis. Academic Press, London. 483 pp.
16. Hayman, D. S. 1982. The physiology of vesicular-arbuscular endomycorrhizal symbiosis. Can J. Bot. 6:944-963.
17. Hussey, R. S., and Roncadori, R. W. 1982. Vesicular-arbuscular mycorrhizae may limit nematode activity and improve plant growth. Plant Dis. 66:9-14.
18. Linderman, R. G. 1985. Microbial interactions in the mycorrhizosphere. Pages 117-120 in: Proc. 6th N. Am. Conf. on Mycorrhizae. R. Molina, ed.
19. MacGuidwin, A. E., Bird, G. W., and Safir, G. R. 1985. Influence of *Glomus fasciculatum* on *Meloidogyne hapla* infecting *Allium cepa*. J. Nematol. 17:389-395.
20. Mengel, K., and Kirkby, E. A. 1979. Principles of Plant Nutrition. International Potash Institute, Bern, Switzerland. 593 pp.
21. Pacovsky, R. S., Bethelenfalvay, G. J., and Paul, E. A. 1986. Comparisons between P-fertilized and mycorrhizal plants. Crop Sci. 26:151-156.
22. Paul, E. A., and Kucey, R. M. N. 1981. Carbon flow in plant microbial associations. Science 213:473-474.
23. Ratnayake, M., Leonard, R. T., and Menge, J. A. 1978. Root exudation in relation to supply of phosphorus and its possible relevance to mycorrhizal formation. New Phytol. 81:543-552.
24. Reid, C. P. P. 1984. Mycorrhizae: A root-soil interface in plant nutrition. Pages 29-50 in: Microbial-Plant Interactions, ASA Special Pub. 47. R. L. Todd and J. E. Giddens, eds.
25. Ross, J. P. 1972. Influence of endogone mycorrhiza on Phytophthora root rot of soybean. Phytopathology 62:896-897.
26. Schenck, N. C., and Kellam, M. K. 1978. The influence of vesicular-arbuscular mycorrhizae on disease development. Fla. Agric. Exp. Stn. Bull. 798.
27. Smith, G. S. 1987. Interaction of nematodes with mycorrhizal fungi. Pages 133-143 in: Society of Nematology Vistas. J. A. Veech and D. W. Dickson, eds.
28. Smith, G. S., Hussey, R. S., and Roncadori, R. W. 1986. Penetration and post-infection development of *Meloidogyne incognita* as affected by *Glomus intraradices* and phosphorus. J. Nematol. 18:429-435.
29. Smith, G. S., Roncadori, R. W., and Hussey, R. S. 1986. Interaction of endomycorrhizal fungi, superphosphate, and *Meloidogyne incognita* on cotton in microplot and field studies. J. Nematol. 18:208-216.
30. Thompson Cason, K. M., Hussey, R. S., and Roncadori, R. W. 1983. Interaction of vesicular-arbuscular mycorrhizal fungi and phosphorus with *Meloidogyne incognita* on tomato. J. Nematol. 15:410-417.
31. Wallace, H. R. 1973. Nematode Ecology and Plant Disease. Oxford, Alden Press. 228 pp.
32. Wallace, H. R. 1983. Interactions between nematodes and other factors on plants. J. Nematol. 15:221-227.
33. Zambolin, L., and Oliveira, A. A. R. 1986. Interacaco entre *Glomus etunicatum* and *Meloidogyne javanica* em feijao (*Phaseolus vulgaris* L.). Fitopatologia Brasileira 11:217-226.